

RHIZOMYIDAE FROM THE LOWER MANCHAR FORMATION
(MIOCENE, PAKISTAN)WILMA WESSELS¹HANS DE BRUIJN¹

ABSTRACT

Miocene deposits from several areas of Pakistan have produced a good record of Rhizomyid rodents. Study of the Rhizomyidae (with one new species: *Prokanisamys major*) from twelve localities from the lower Manchar Formation in Sind shows a rapid diversification of this family during their early history. The pattern of occurrences of Rhizomyidae species suggests that they can be used in biozones.

KEY WORDS: Miocene, rodents, Pakistan, Rhizomyidae

INTRODUCTION

Miocene deposits of Pakistan have produced a good record of rhizomyid rodents. Often more than one species is present per locality. Study of the rhizomyid material from twelve assemblages in the Lower Manchar Formation (Lower and Middle Miocene) in combination with the results obtained by Flynn (1982a, 1986) on the basis of material from Middle and Upper Miocene levels of the Potwar Plateau indicates that this family is suitable for biostratigraphy.

Detailed information on the systematics of the Rhizomyidae from the Lower Manchar Formation will be given in the first part of this paper. The Miocene record and the age of the Lower Manchar occurrences of the Pakistani Rhizomyidae will be discussed subsequently.

The material discussed below was collected within the framework of the project "Cenozoic Mammals of Pakistan," a collaborative program of Howard University (Washington, DC), the Geological Survey of Pakistan (Quetta) and the University of Utrecht (the Netherlands), during the field seasons of 1981-1984 (Fig.1). De Bruijn and Hussain (1984) presented a provisional overview of the successive rodent assemblages collected in 1981 and 1982. The Thryonomyidae were discussed by de Bruijn and Hussain (1985), the Ctenodactylidae by de Bruijn et al. (1989), and the Myocricetodontinae by Wessels et al. (1987) and Wessels (1996). Despite meager stratigraphical information on the assemblages from four successive levels sampled in the Lower Manchar Formation, one kilometer to the north of the Sehwan Sharif section (Wessels, 1996), the fossils collected from this section will be studied. Locality H-GSP 84.24 is the stratigraphically lowest assemblage and H-GSP 84.27 the highest in that section.

Classification of the Rhizomyidae follows Chaline, Mein and Petter (1977). The nomenclature of parts of cheek teeth is as in Wessels (1996), who follows Mein and Freudenthal (1971) except for minor changes.

Measurements of length, width and height of cheek teeth were taken with a

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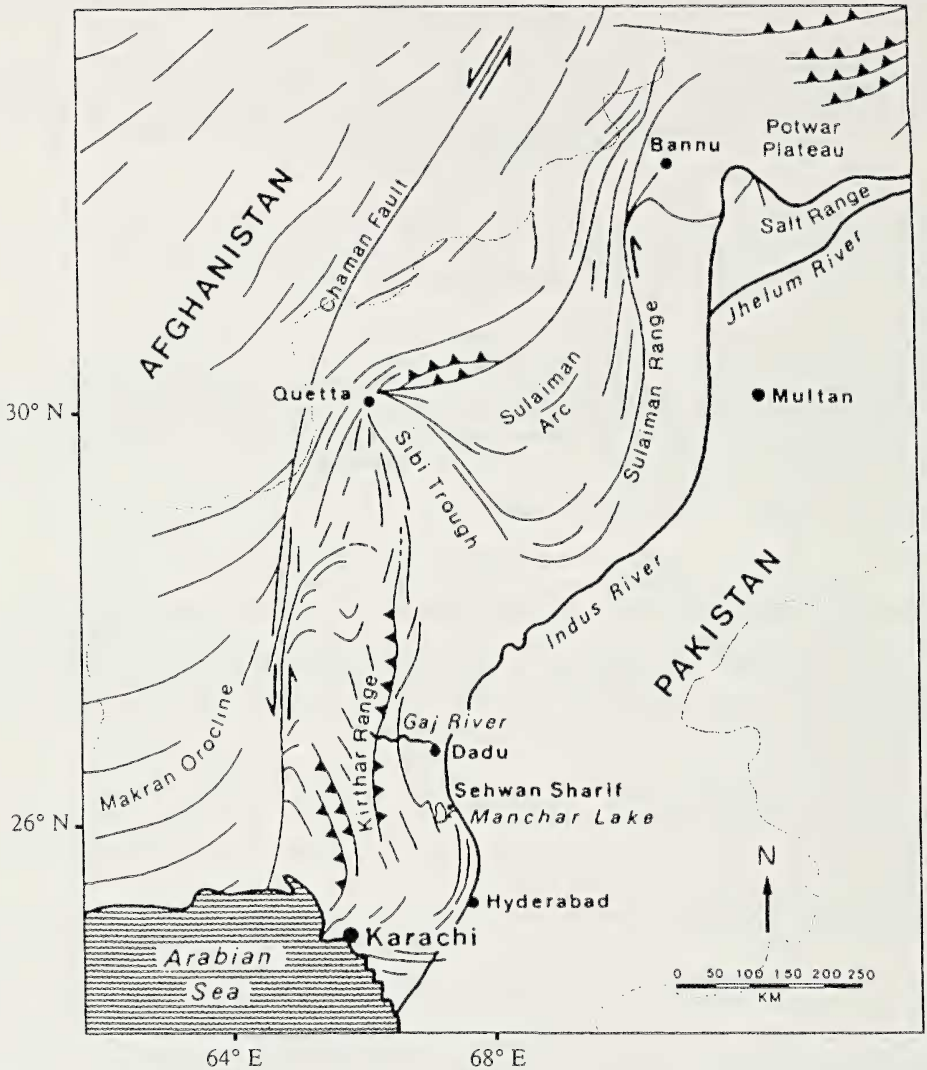


Fig. 1.—Sketch map of south-western Pakistan showing the major tectonic features and the position of localities mentioned in the text (after Sarwar and de Jong, 1979).

Leitz Ortholux measuring microscope. All measurements are given in 0.1-mm units.

SYSTEMATIC PALEONTOLOGY

Family Rhizomyidae Miller and Gidley, 1918

Introduction

The family Rhizomyidae is divided into two subfamilies: the Tachyoryctinae (African mole rats) and the Rhizomyinae (Asiatic bamboo rats). Extensive infor-

mation and references on extant and fossil members of this family can be found in the following: Carleton and Musser (1984); Flynn (1982, 1986, 1990); Nowak (1991); and Nevo (1999).

Black (1972) reviewed the fossil Rhizomyidae from Pakistan and India and recognized two groups. One group, containing the genera *Kanisamys* and *Protachyoryctes*, was thought to be related to the African *Tachyoryctes* and the other, containing *Rhizomyoides* (now *Brachyrhizomys*), was considered ancestral to the Asiatic genera *Rhizomys* and *Cannomys*. Finds of *Prokanisamys arifi*, which supposedly is the direct ancestor of *Kanisamys* (de Bruijn et al., 1981), strengthens the idea proposed by Black. The extensive systematic revision of the Rhizomyidae by Flynn (1982a), based on material from the Miocene of the Potwar Plateau, confirmed the idea that the Tachyoryctinae are of Asiatic origin (Flynn, 1982a,b; 1986). *Brachyrhizomys*, the first true Rhizomyinae, showing adaptations to a fossorial way of life, appears in the Potwar Plateau in a locality dated at approximately nine Ma. The quick diversification of *Brachyrhizomys* that followed has been interpreted as the result of their fossorial lifestyle (Flynn, 1982a).

Taxonomy

Prokanisamys de Bruijn, Hussain and Leinders, 1981

Original diagnosis.—"Cricetid with incipiently hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially rather than anterolabially as in most post-Oligocene cricetids. The M_3 is smaller than the M_1 . The connection between the anteroloph and the protocone of M^1 is a strong ridge along the lingual border of that tooth."

Emended Diagnosis.—Small, slightly hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially or transversely rather than anterolabially as in most post-Oligocene cricetids. The M_3 is shorter than the M_1 ; the M_3 shows a large variation in width measurements.

Type Species.—*Prokanisamys arifi* de Bruijn, Hussain and Leinders, 1981.

Other Species Included.—*Prokanisamys benjavuni* (Mein and Ginsburg, 1985); *Prokanisamys kowalskii* (Lindsay, 1996); *Prokanisamys major* nov sp.; ?*Prokanisamys* sp A.

Prokanisamys arifi de Bruijn, Hussain and Leinders, 1981 (Fig. 2A–T)

Type Locality.—H-GSP 116.

Type Level.—Murree Formation.

Original Diagnosis.—"Cricetid with incipiently hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially rather than anterolabially as in most post-Oligocene cricetids. The M_3 is smaller than the M_1 . The connection between the anteroloph and the protocone of M^1 is a strong ridge along the lingual border of that tooth."

Emended Diagnosis.—Cricetid with slightly hypsodont cheek teeth. The hypolophulid of the lower molars is directed postero-labially or transverse. The M_3 is smaller than the M_1 . The anterolophule, a strong ridge connecting anterocone and protocone on the antero-lingual edge of the M^1 , outlines a clear protosinus.

Occurrences.—Kohat, Murree Formation, Banda daud Shah; locality H-GSP 116 (de Bruijn et al., 1981); Zinda Pir Dome, Chitarwata Formation and Vihowa

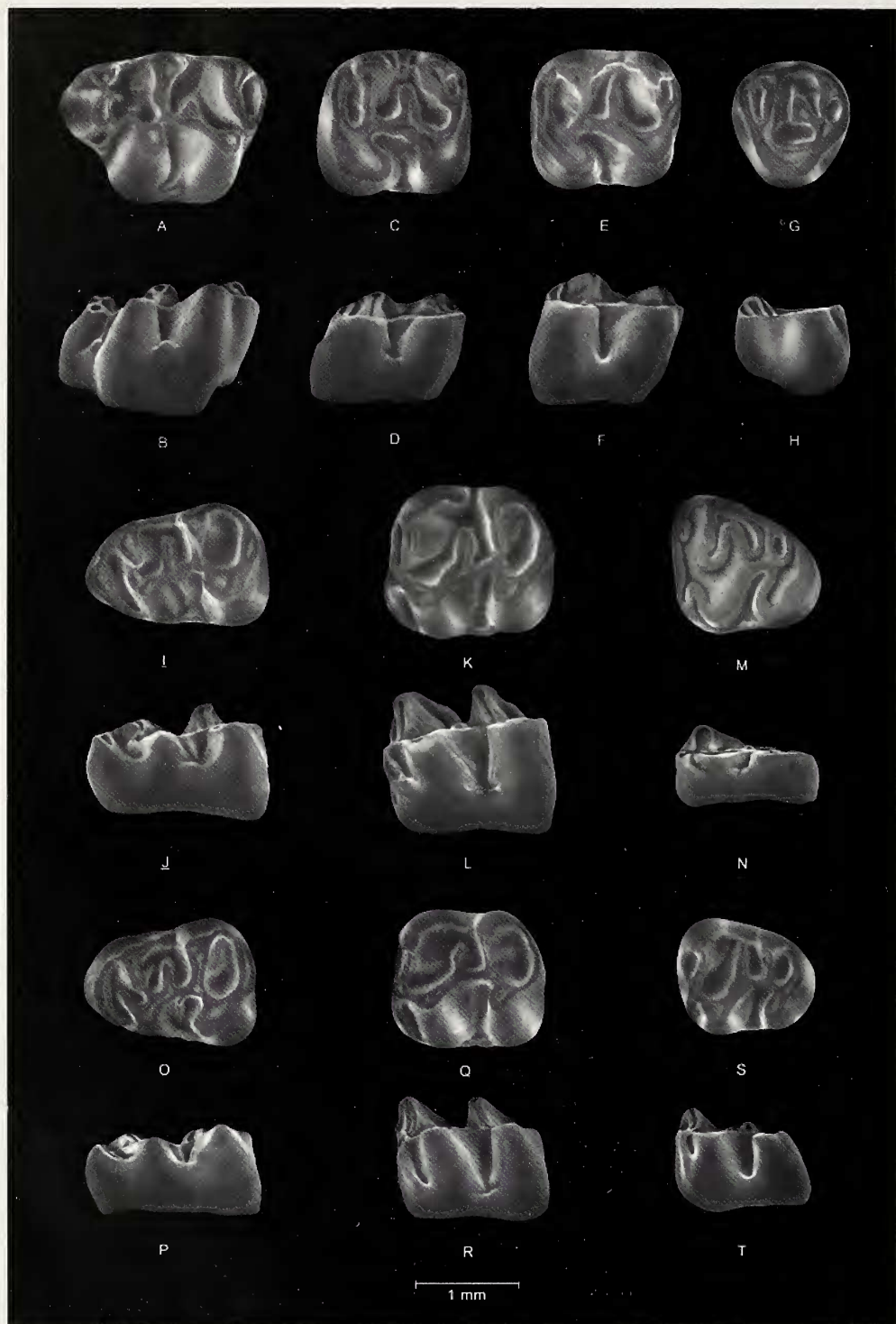


Fig. 2.—*Prokanisamys arifi* from H-GSP 8311. A,B. Occlusal, labial views M^1 , H-GSP 8311/4359. C,D. Occlusal, labial views M^2 , H-GSP 8311/4363. E,F. Occlusal, labial views M^2 , H-GSP 8311/4369. G,H. Occlusal, labial views M^3 , H-GSP 8311/4381. I,J. Occlusal, labial views M_1 , H-GSP 8311/4303. K,L. Occlusal, labial views M_2 , H-GSP 8311/4311. M,N. Occlusal, labial views M_3 , H-GSP 8311/4331. O,P. Occlusal, labial views M_1 , H-GSP 8311/4294. Q,R. Occlusal, labial views M_2 , H-GSP 8311/4316. S,T. Occlusal, labial views M_3 , H-GSP 8311/4334. Letters underlined: original is from the right side.

Formation, localities Z 126, Z 122, Z 120, Z 124 (Lindsay and Downs, 1998); Sind, Lower Manchar Formation, Sehwan section, localities H-GSP 8114a, 8114, 8424, 8426; Sind Lower Manchar Formation, Gaj River section, localities H-GSP 8107(a), 8311, 8106.

Material and Measurements.—Figure 3 and Appendix 1, Appendices 7–11.

Comparisons and Discussion.—Small changes in morphology through time can be seen in *P. arifi*. In the upper and lower molars from the Murree locality the longitudinal crest is semi-circular, in the somewhat younger localities from the Manchar Formation several *P. arifi* specimens show a more obliquely directed longitudinal crest. In the youngest occurrences, an obliquely directed longitudinal crest (and therefore a deeper sinus(id)) is common. The *P. arifi* specimens from the younger localities (H-GSP 8114a, 8424, 8114, 8426) have slightly higher crowned upper molar crowns and the lower molars bear plumper cusps. The slightly forward-directed mesolophid (in the Murree specimens) becomes more transverse in specimens from younger localities. The lingual branch of the anterocoonid becomes stronger and higher through time (the connection between anterocoonid and metaconid becomes stronger). Minor changes in size occur also: the M^2 becomes broader and the M_3 larger through time.

The roots of *P. arifi* from the Murree Formation (loc. 116) are only known on M^2 (which has four roots). M^2 of *P. arifi* from H-GSP 8311 has four roots also and M^1 has three roots (the broad lingual root has a deep central groove).

Prokanisamys arifi primarily differs from *P. major* in being smaller and relatively higher.

Lindsay (1996) described *Eumyarion kowalskii*, a species closely resembling *Prokanisamys arifi*. He considered *E. kowalskii* to be the predecessor of *P. arifi* because *E. kowalskii* is lower-crowned than *P. arifi*, was found in a stratigraphically lower level and does not co-occur with *P. arifi*.

The species *Eumyarion kowalskii* Lindsay (1996) is transferred to the genus *Prokanisamys* because the type material from the Chitarwata Formation is metrically as well as morphologically much closer to that S. E. Asiatic genus than to the *Eumyarion* from Europe and western Asia. Although the genera *Prokanisamys* and *Eumyarion* are superficially similar and show the same microstructure of the incisor enamel (Kalthoff, 1999), their cheek teeth show consistent differences (Fig. 4, Table 1 and Appendix 2). In all respects listed the species *kowalskii* fits *Prokanisamys*. Since there is no good reason to assume that *Prokanisamys* is closely related to *Eumyarion*, we prefer to classify this genus with the Rhizomyidae and not with the Eumyarioninae (Ünay, 1989) as suggested in Lindsay (1996).

With the elimination of *Eumyarion* from the record of the Indian subcontinent the number of Miocene cricetid genera shared with Europe during the Miocene is reduced to one (the *Spano-Democraticetodon* group of species).

Although *Prokanisamys kowalskii* is found in stratigraphically older sediments than *P. arifi*, enhancing the suggestion that *P. kowalskii* may have given rise to *P. arifi* (Lindsay, 1996:285), its relationship to *P. arifi* is not clear. *P. kowalskii* cheek teeth seem to have lower crowns (primitive), but the metalophid of the M_1 is transverse in some specimens (derived), they are much larger than *P. arifi* and the M_1/M_3 width ratio (Appendix 7) is lower than in *P. arifi* from the Murree (derived). Moreover the co-occurrence of several *Prokanisamys* species in slightly younger localities indicates a complex evolutionary pattern rather than simple ancestor-descendant relationships.

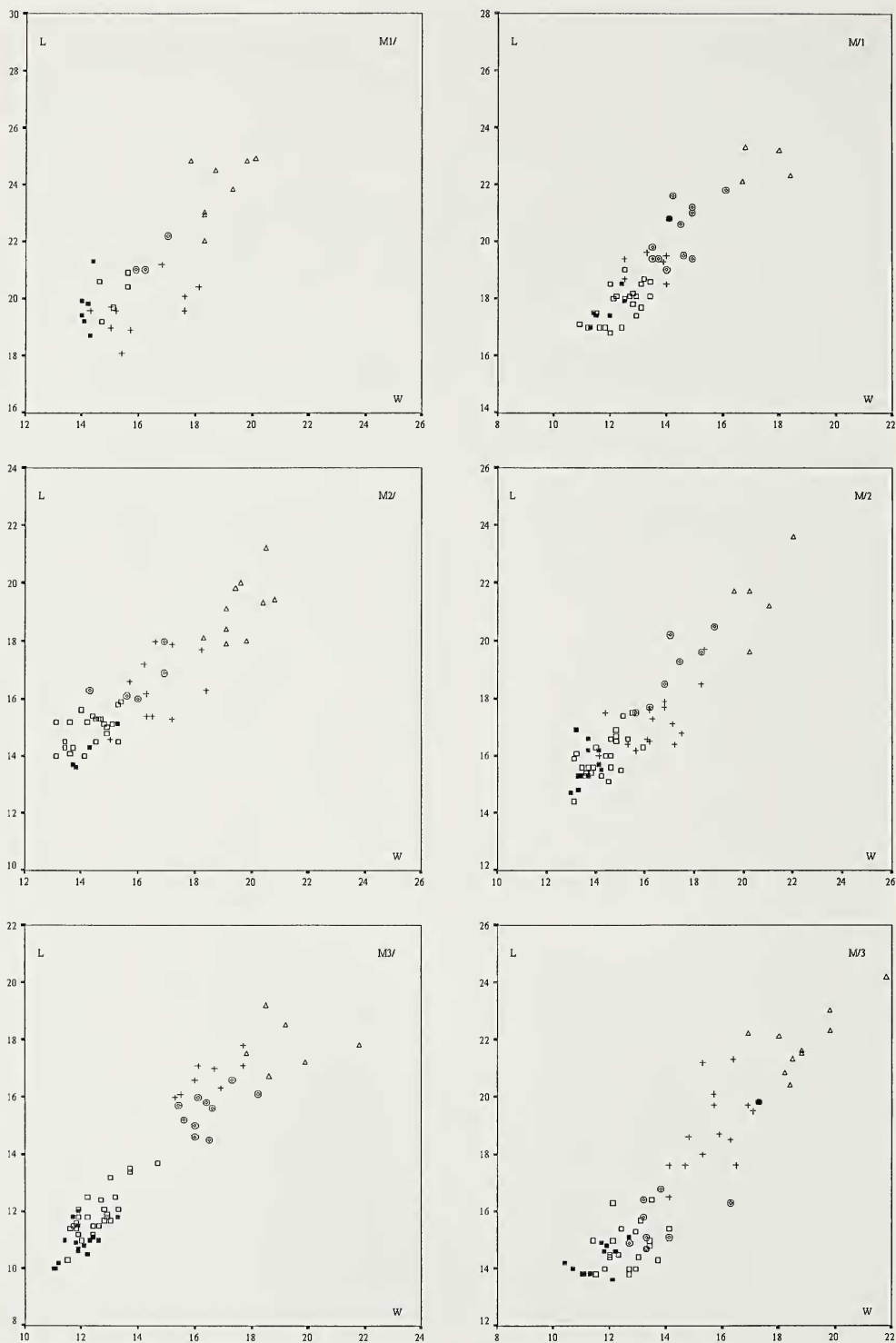


Fig. 3.—Scatter diagrams of tooth length and width of **■***Prokanisamys arifi* from the Murree FM and **□***Prokanisamys arifi* from other localities, **⊙***Prokanisamys major*, **+***Prokanisamys benjavuni*, **●***?Prokanisamys* sp. A and **△***Kanisamys indicus* from the Lower Manchar FM.

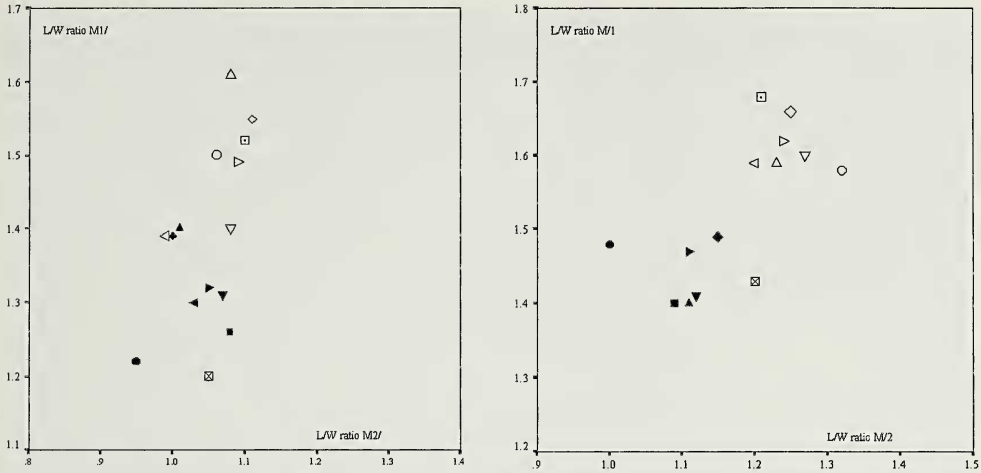


Fig. 4.—Scatter diagrams of L/W ratios of \triangleleft *Eumyarion medium*, Sansan; ∇ *Eumyarion latior*, Aliveri; \square *Eumyarion bifidus*, Sandelzhausen; \diamond *Eumyarion bifidus*, Puttenhausen; \triangleright *Eumyarion montanus*, Kesseköy; Δ *Eumyarion carbonicus*, Harami 1; \circ *Eumyarion aff. carbonicus*, Harami 3; \blacklozenge *Prokanisamys arifi*, H-GSP 116; \blacktriangleright *Prokanisamys arifi*, H-GSP 8311; \blacktriangledown *Prokanisamys major* n. sp., H-GSP 8224; \blacktriangleleft *Prokanisamys major*, H-GSP 8114; \boxtimes *Prokanisamys benjavuni*, Li; \bullet *Prokanisamys benjavuni*, H-GSP 8114; \blacksquare *Prokanisamys benjavuni*, H-GSP 8424; \blacktriangle *Prokanisamys kowalskii*, Z 113.

***Prokanisamys major*, new species**
(Fig. 5A–L)

Derivatio nominis.—“major” because the cheek teeth are large.

Holotype.— M^1 sin no. 4522, 21.0–16.2 (Fig. 5C–D).

Type Locality.—H-GSP 8114.

Type Level.—Lower Manchar Formation (Middle Miocene).

Occurrences.—Sind, Lower Manchar Formation, Sehwan section, localities H-GSP 8106, 8114, 8227, 8224, 8424, 8214.8425, 8426, 8427; Potwar Plateau: Y-GSP 591, 592, 642, 501, 589, 491, 640, 641, 496, 634 (Flynn, 1986).

Diagnosis.—*Prokanisamys major* represents a large *Prokanisamys* with the main cusps clearly distinguishable; the lophs are (in fresh specimens) lower than

Table 1.—Summary of the major morphological differences between *Eumyarion* and *Prokanisamys* species.

<i>Eumyarion</i>	<i>Prokanisamys</i>
M^1 and M^2	M^1 and M^2
1) Metalophule transverse connecting to hypocone	1) Metalophule posteriorly connected to postero-loph
2) Anterior arm of protocone often present in M^1	2) Anterior arm of protocone never present
3) Metacone inflated	3) Metacone not inflated
M_1 and M_2	M_1 and M_2
1) Posterior arm of protoconid and mesolophid usually present	1) Never two ridges in the mesosinusid present (never a posterior arm of protoconid and a mesolophid)
2) Free ending posterior arm of the hypoconid usually present	2) Free ending posterior arm of hypoconid never present
3) Entoconid inflated	3) Entoconid not inflated

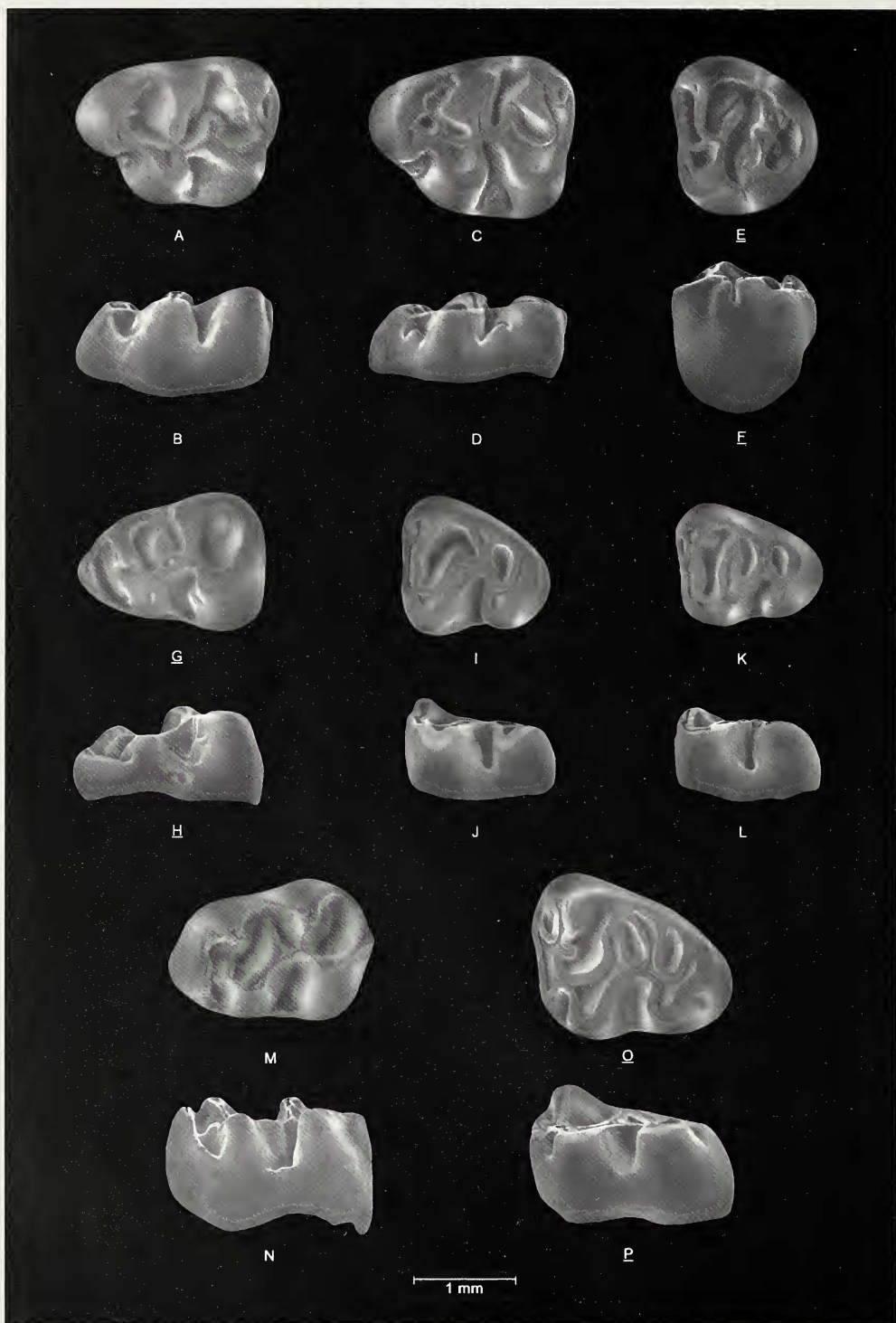


Fig. 5.—*Prokanisamys major* from H-GSP 8114. A,B. Occlusal, labial views M^1 , H-GSP 8114/4521. C,D. Occlusal, labial views M^1 , H-GSP 8114/45223. E,F. Occlusal, labial views M^3 , H-GSP 8114/4557. G,H. Occlusal, labial views M^1 , H-GSP 8114/4582. I,J. Occlusal, labial views M^3 , H-GSP 8114/4612. K,L. Occlusal, labial views M^3 , H-GSP 8114/4614. *?Prokanisamys* sp. A from H-GSP 8107(a). M,N. Occlusal, labial views M^1 , H-GSP 8107a/4015. O,P. Occlusal, labial views M^3 , H-GSP 8107/4068. Letters underlined: original is from the right side.

the cusps and the M_3 is shorter than the M_1 . The anterolophid is not or poorly connected to the anteroconid. The metalophulid, hypolophulid, protolophule and metalophule are short.

Differential Diagnosis.—*Prokanisamys major* specimens are morphologically similar to *P. arifi*, larger (although a slight overlap may occur) and relatively lower crowned.

Prokanisamys major differs from *P. benjavuni* in having larger first molars, smaller third molars, the M^1 and M^2 are relatively narrower, the molars are more cusped (especially the lower), the M^1 has a protosinus and the labial cusps in the lower molars lack an antero-labial ridge.

Prokanisamys major specimens are morphologically close to *P. kowalskii*. Although the size-range of *P. kowalskii* and *P. major* overlap, except for the M^1 and the third molars and the largest *P. major* specimens, *P. major* is considered to represent a different species because the mean size of *P. kowalskii* specimens is larger than the mean sizes of *P. major* from the older localities. Furthermore the M^3 of *P. kowalskii* is much smaller than in *P. major* whereas the M^1 is larger and the M_3 much larger.

Material and Measurements.—Figure 3 and Appendix 3, Appendices 7–11.

Description of the Type Material.— M^1 . The cusps are bulbous; height of molars moderate; anterocone short and crescent shaped; the two anterocone cusps are slightly separated; the lingual cusps are slightly compressed transversally and a protosinus is present; the protocone is weak or poorly connected to protolophule or longitudinal crest; the mesoloph is short and transverse or directed slightly posteriorly; the postero-sinus is present and persists in worn specimens. In the holotype, a small cusp is present on the antero-lingual base of the hypocone. The slightly curved sinus is directed forwards.

M^2 . The anterior part of this molar is missing. The cusps are bulbous; the height is moderate; lingual cusps are slightly compressed transversally; the longitudinal crest is oblique; the mesoloph short; the postero-sinus is less developed than in the M^1 and disappears through wear; the sinus is slightly curved forwards and does not extend anteriorly of the protolophule.

M^3 . The cusps are clearly defined in unworn specimens; the labial branch of the anteroloph is preserved in fresh specimens only; the mesoloph is short; the posteroloph is well developed; the metacone is clearly visible; the paracone, the longitudinal crest and the hypocone are connected in advanced wear stages.

M_1 . The cusps are bulbous; the lophes are lower than the cusps; the anteroconid is simple and connected to the metaconid by a short but high lingual branch of the anterolophid; the anterolophulid is poorly or weakly developed in all specimens and not connected to the anteroconid. The metalophulid is always short, transverse or slightly backwards directed and poorly connected to protoconid. The longitudinal crest is directed obliquely towards the entoconid; the hypolophulid is short. The hypoconid is in three specimens weakly connected to the longitudinal crest. The mesolophid is short; a short ridge on the postero-lingual edge of the metaconid descends to the base of the mesosinusid; the posterolophid is strong; the sinusid directed backwards.

M_2 . The cusps are bulbous; the lophes are lower than the cusps; the lingual branch of the anterolophid is absent and the labial branch is short; the longitudinal crest is obliquely directed; the metalophulid, hypolophulid and mesolophid are short and transverse. A short ridge on the postero-lingual edge of the metaconid descends to the base of the mesosinusid; the posterolophid is strong; the sinusid is transverse.

M_3 . The cusps are bulbous; the lophes are lower than cusps; the very short branches of the anterolophid disappear with wear; the metalophulid and hypolophulid are short; the longitudinal crest is strong and obliquely directed; the mesolophid is either of medium length or reaches the lingual edge; a clear postero-sinusid is present; the sinusid is transverse or directed posteriorly.

Comparisons and Discussion.—*Prokanisamys major* and *P. arifi* differ in size, but an overlap is present (Fig. 3). *P. major* is relatively lower crowned and slightly more robust than *P. arifi*. The cusped nature of especially the lower molars of *Prokanisamys major* distinguishes these from specimens of *P. benjavuni*. The labial cusps in the lower molars of *Prokanisamys major* do not have an antero-

labial ridge and the upper molars do not have a ridge on the antero-lingual side of the lingual cusps. The M^1 of *P. major* has a protosinus, which is lacking in *P. benjavuni*. The M^2 and M^3 of *P. major* and *P. benjavuni* are more difficult to distinguish than the lower molars because they have a similar degree of hypsodonty. Moreover, the variation in surface area is large due to differences between wear stages (Appendix 9).

P. major is lower crowned than *P. kowalskii* (Lindsay, 1996). *P. major* differs from *P. kowalskii* in size, and in having a more obliquely directed longitudinal crest, a short and transverse protolophule in the M^1 ; the protocone is often poorly connected to the longitudinal crest, and anterolophulid and metalophulid (M_1) are weakly developed.

Prokanisamys major differs from *Kanisamys indicus* in being smaller, less hypsodont and in having the cricetid bunodont pattern.

Prokanisamys major is represented by 71 specimens from seven localities. In the younger assemblages the molars are slightly larger and the upper molars are relatively higher, the labial branch of the anteroloph (M^2) is stronger and may end in a small cuspule, and the posterolophid is stronger.

Prokanisamys major and *P. arifi* share a similar morphology, but *P. major* is larger and lower crowned and is therefore not considered to be a direct descendant from *P. arifi*. Also *P. kowalskii* and *P. major* have a similar morphology, but *P. major* is not considered to be a descendant of *P. kowalskii* because of differences in relative sizes of the cheek teeth. Most cheek teeth of *P. kowalskii* are larger than those of the geologically oldest specimens of *P. major* (Appendices 3, 9 and 10).

Prokanisamys benjavuni (Mein and Ginsburg, 1985)
(Fig. 6A–P)

Type Locality.—Li basin, Thailand.

Type Level.—Miocene.

Diagnosis.—“Espèce du genre *Prokanisamys* différant de *Prokanisamys arifi* par des M^1 plus petites et des M^3 plus grandes, une hypsodontie plus forte tout en restant modérée, des surfaces occlusales peu concaves par suite du développement de la lophodontie. Grande réduction de l'antérolophide qui disparaît même complètement sur M_3 . Hypolophulides jamais oblique vers l'arrière.” (Mein and Ginsburg, 1997).

Addition to Diagnosis.—The anterocone and protocone are strongly connected by the lingual branch of the anteroloph; a protosinus is absent. In *Prokanisamys benjavuni* the M^1 is relatively broader, the M^2 larger and the M^3 and M_3 are much larger than in *P. arifi*. The M_1 has a narrow anteroconid-complex. The cheek teeth are more lophate than *P. arifi*.

Occurrences.—Li Basin, Thailand (Mein and Ginsburg, 1985, 1997); Bugti area, in levels 5 and 6 (Welcomme and Ginsburg, 1997); Sind, Lower Manchar Formation, Sehwan section, localities H-GSP 8114a, 8114, 8424, 8426.

Material and Measurements.—Figure 3 and Appendix 4, Appendices 7–11.

Comparisons and Discussion.—Although the variation in size (especially M_3) is large in the Li material, Mein and Ginsburg concluded that only one species is present. They considered the size variation to be the result of wear: hypsodont molars become shorter and broader when worn.

The specimens from Pakistan are on average slightly larger than those from

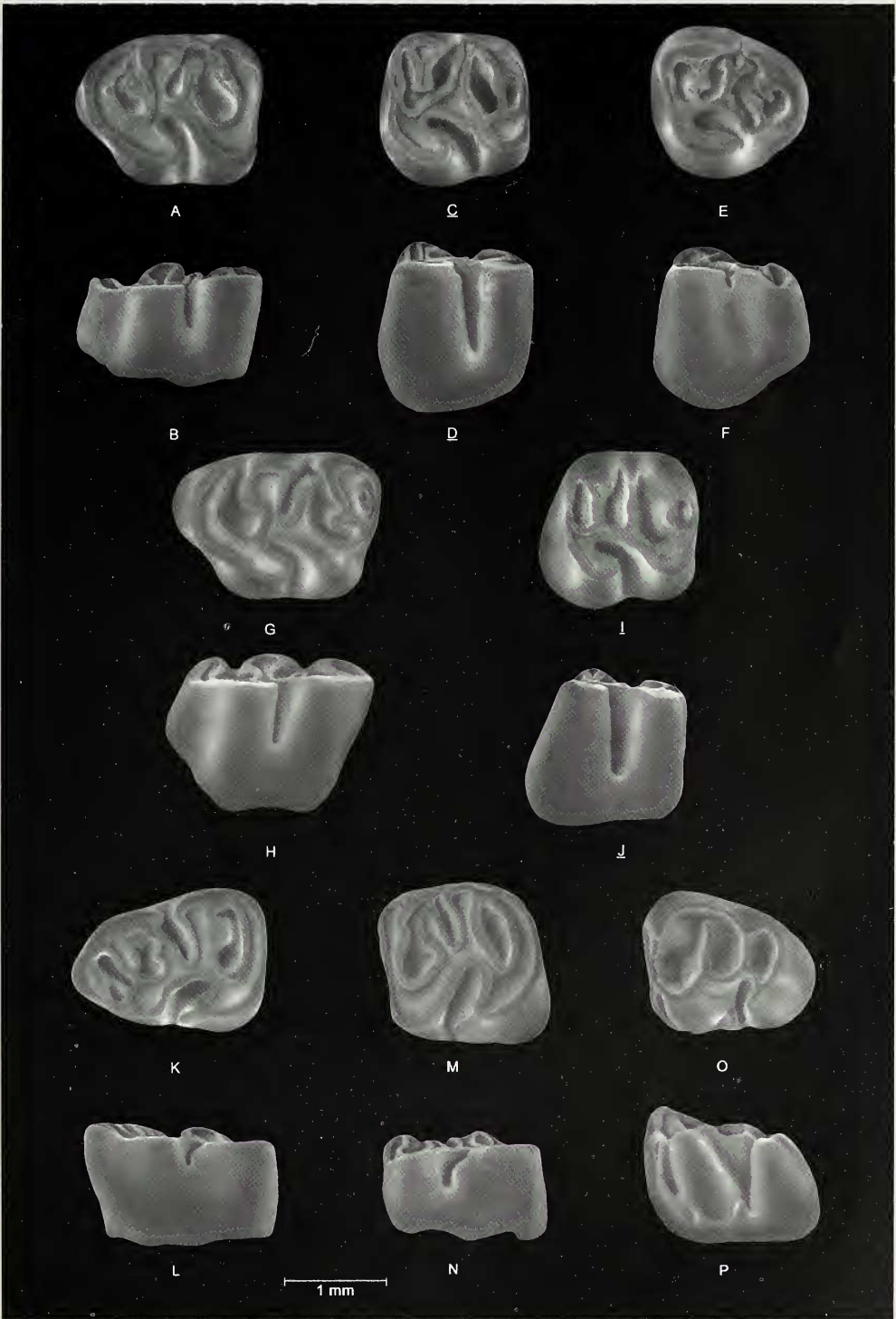


Fig. 6.—*Prokanisamys benjavuni* from H-GSP 8114. A,B. Occlusal, labial views M^1 , H-GSP 8114/4523. C,D. Occlusal, labial views M^2 , H-GSP 8114/4543. E,F. Occlusal, labial views M^3 , H-GSP 8114/4554. G,H. Occlusal, labial views M^1 , H-GSP 8114/4524. I,J. Occlusal, labial views M^2 , H-GSP 8114/4542. K,L. Occlusal, labial views M_1 , H-GSP 8114/4577. M,N. Occlusal, labial views M_2 , H-GSP 8114/4593. O,P. Occlusal, labial views M_3 , H-GSP 8114/4618. Letters underlined: original is from the right side.

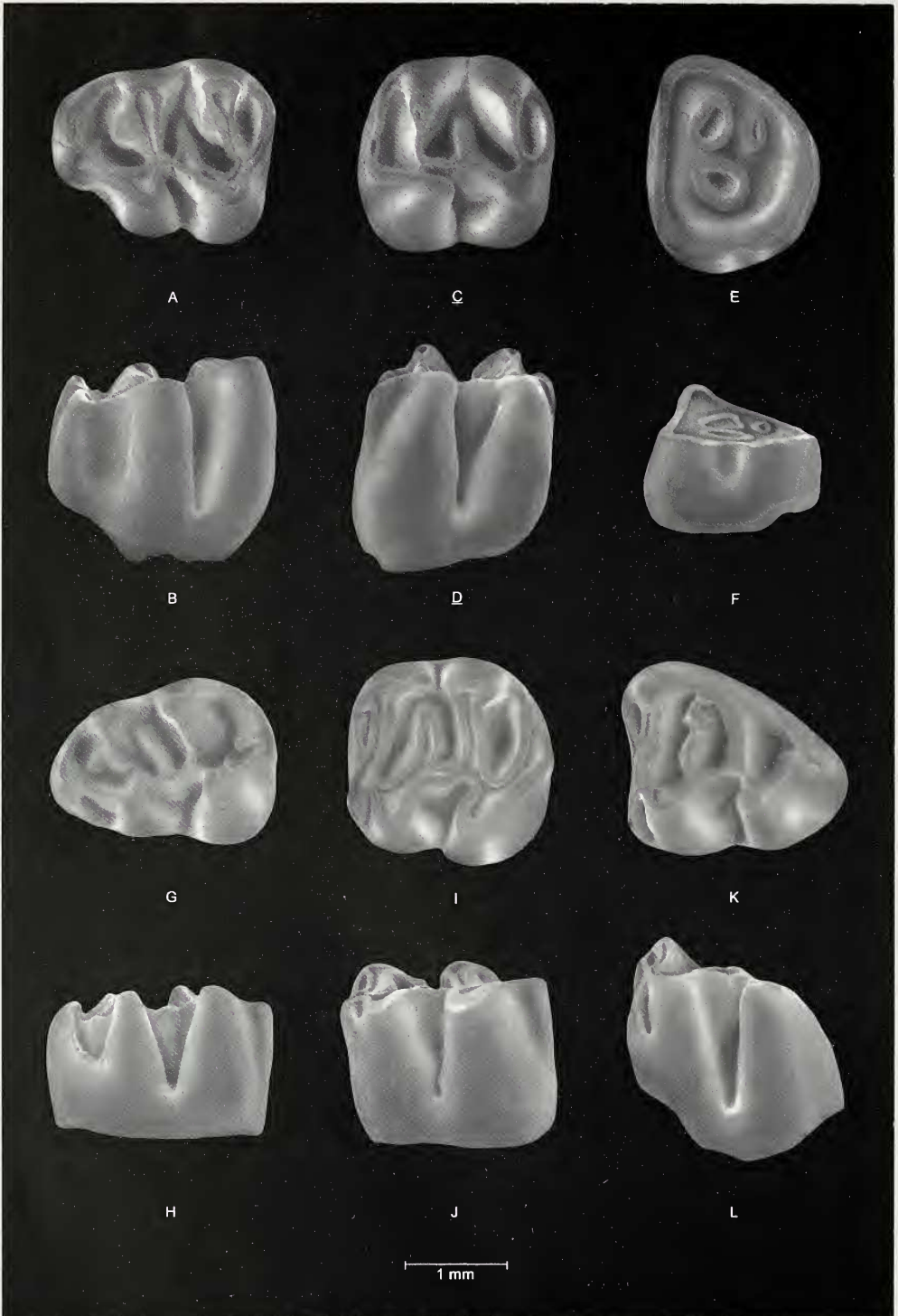


Fig. 7.—*Kanisamys indicus* from H-GSP 8224. A,B. Occlusal, labial views M^1 , H-GSP 8224/4502. C,D. Occlusal, labial views M^2 , H-GSP 8224/4517. E,F. Occlusal, labial views M^3 , H-GSP 8224/4524. G,H. Occlusal, labial views M_1 , H-GSP 8224/4542. I,J. Occlusal, labial views M_2 , H-GSP 8224/4556. K,L. Occlusal, labial views M_3 , H-GSP 8224/4575. Letters underlined: original is from the right side.

Thailand. M^1 and M^2 are broader and the M^3 is relatively larger. The lower molars are slightly larger (M_2 and M_3) or within the upper range of the specimens from Li (M_1). The Pakistani specimens are morphologically similar to those of Thailand, but the M_3 specimens show a wider morphological variation. The roots of the specimens from both areas are the same. M^1 has a broad lingual root with a deep groove in its center and the M^2 has four roots.

Flynn (1986) and Jacobs et al. (1989) have reported *Prokanisamys benjavuni* from some localities from the Potwar Plateau. However, the specimens figured in Jacobs et al. (1989) and casts thereof clearly represent *Prokanisamys major*. Mein and Ginsburg (1997) already observed important differences between the Thai and the Potwar Plateau material assigned to *P. benjavuni*, and correctly concluded that these do not belong to the same lineage.

Prokanisamys benjavuni and *Brachyrhizomys* species (Potwar Plateau, nine Ma, Flynn, 1982a) have some characteristics in common: the shape of the M^1 , which lacks a protosinus (flexus or anterior sulcus in Flynn, 1982a), and the deep sinusid in the lower molars. *Prokanisamys benjavuni* is much smaller and only slightly hypsodont, but its cheek-teeth morphology suggests it could belong to the same lineage as *Brachyrhizomys*. If that is so, the separation between the Rhizomyinae and the Tachyoryctinae is older than previously thought. The 'sudden' occurrence of several *Brachyrhizomys* species in the Nagri Formation and Dhok Pathan Formation from the Potwar Plateau (Flynn, 1982a) could be interpreted as the result of a rapid diversification of this genus after its immigration from a more eastern region.

?*Prokanisamys* sp.A
(Fig. 5M–P)

Occurrences.—Sind, Lower Manchar Formation, Sehwan section; locality H-GSP 8107(a).

Material and measurements.—Figure 3 and Appendix 5, Appendices 7–11.

Description of the Material.—The single M^1 is severely damaged and shows a clear protosinus, but no further detail. The lower molars have low bulbous cusps. The lophes are lower than the cusps. The anteroconid of the M_1 is connected to the metaconid by the low lingual branch of the anterolophid. On the M_2 the anterolophid has two well-developed branches. The mesolophid is of medium length.

Comparisons and Discussion.—This very large *Prokanisamys* is larger than most *Prokanisamys major* specimens from younger localities. The teeth are cusped and have low crowns, typical of *Prokanisamys*. ?*Prokanisamys* sp.A differs from *P. kowalskii* in having a more obliquely directed longitudinal crest (M^1) and in the interrupted protoconid-anteroconid connection (M_1). The transverse metalophid is directed towards the anterior part of the protoconid, but not connected to it. ?*Prokanisamys* sp.A differs from *P. major* in having a larger and higher M^1 , M_1 . This species may be seen as a descendant of *P. kowalskii* (Lindsay, 1996). The teeth are within the size-range of that species but they seem to be more hypsodont and the M_1 has a more anteriorly directed metalophid (derived characters). The M_1/M_3 length-ratio is larger than 1.0, which is a *Kanisamys* characteristic. These few teeth with a cusped cricetid dental pattern and a M_1/M_3 length-ratio as in *Kanisamys* seem to represent a new species. We refer this species as ?*Prokanisamys* sp.A because the material is considered insufficient as the basis for a formal name.

Kanisamys Wood, 1937

Type Species.—*Kanisamys indicus* Wood, 1937.

Other Species Included.—*Kanisamys sivalensis* Wood, 1937; *Kanisamys nagrii* Prasad, 1968; *Kanisamys potwarensis* Flynn, 1982a.

Diagnosis.—"Small tachyoryctines with moderate to advanced hypsodonty and lophodonty; lower massetric crest strongly inclined; mesolophids become reduced through time but are distinct; incisors small with strongly rounded enamel; dentary depth shallow" (Flynn, 1982a).

Kanisamys indicus Wood, 1937

(Fig. 7A–L)

Type Locality.—South of Chinji (see Wood, 1937 and Black, 1972).

Type Level.—Chinji Formation.

Original Diagnosis.—"Smallest known *Kanisamys*, lophodont but with recognizable cusps; crown height is moderate; mesolophid and hypolophid usually strong and separate in all lower molars; anterolophid of unworn M₂₋₃ strong and with distinct labial arm; Incisor with two ridges" (Flynn, 1982a).

Occurrences.—In many localities in the Chinji Formation: Potwar Plateau (Wood, 1937; Black, 1972; Dehm et al., 1982; Jacobs et al., 1989); Trans Indus, Daud Khel (Munthe, 1980); N.W.F.P., Banda Daud Shah (Wessels et al., 1982). Sind H-GSP 8114, 8227, 8224, 8425, 8427, 8214 from the Lower Manchar Formation.

Material and Measurements.—Figure 3 and Appendix 6, Appendices 6–10.

Comparisons and Discussion.—*Kanisamys indicus* cheek teeth are larger and more hypsodont than those of *Prokanisamys major* and *P. benjavuni* although some elements show a slight overlap (Fig. 3). The lophs are more prominent than in *Prokanisamys major*. The M¹ of *K. indicus* has, in contrast to *P. benjavuni*, a protosinus and a transverse or slightly forward-curved sinus, which never reaches the protolophule. *Kanisamys indicus* specimens from H-GSP 82.24 have higher lophs and are relatively higher-crowned than specimens from older localities (H-GSP 8228, 8114).

THE MIOCENE RECORD OF THE RHIZOMYIDAE IN PAKISTAN

The oldest occurrence of the Rhizomyidae is *Prokanisamys kowalskii*, from locality Z 113 (Chitarwata Formation, Zinda Pir Dome; Downing et al., 1993; Lindsay, 1996), a locality which has been assigned a tentative age of 20 Ma (Lindsay, 1996). *P. arifi* occurs in slightly younger assemblages in west-central Pakistan (Chitarwata Formation and Vihowa Formation, Zinda Pir Dome; Downing et al., 1993; Lindsay, 1996) northern Pakistan (Murree Formation; de Bruijn et al., 1981) and southern Pakistan (Lower Manchar Formation; de Bruijn and Hussain, 1984; Fig. 8).

The replacement of *P. kowalskii* by *P. arifi* in assemblages that are only somewhat younger, and the occurrence of several other rhizomyid species in association with *P. arifi* in immediately successive sites suggests a rapid diversification of the Rhizomyidae during their early history (Fig. 8). ?*Prokanisamys* sp. A, which is known from locality H-GSP 8107(a) only, seems to be the descendant of *P. kowalskii*. The phylogenetic relationship between *P. arifi*, *P. kowalskii* and *P. major* is not clear.

Prokanisamys benjavuni, which was originally described from the locality Li

Reconstructed sequence of localities	<i>Prokanisamys arifi</i>	<i>Prokanisamys major</i>	<i>Prokanisamys benjavuni</i>	? <i>Prokanisamys</i> sp. A	<i>Kanisamys indicus</i>
H-GSP 82.14		█		█	█
H-GSP 82.24		█			█
H-GSP 84.27		█			█
H-GSP 82.27		█			█
H-GSP 8426	█		█		
H-GSP 8425		█			█
H-GSP 8114	█		█		
H-GSP 8424		█			█
H-GSP 8114a	█		█		
H-GSP 8106		█			
H-GSP 8311					
H-GSP 8209					
H-GSP 8107(a)				█	

Fig. 8.—Distribution chart of the Rhizomyidae from the Lower Manchar Formation in Sind. The localities are listed in stratigraphical order.

in Thailand (Mein and Ginsburg, 1985; 1997), seems to be an immigrant into Pakistan from the east because all Pakistani records, including the oldest teeth known from level 6 in the Dera Bugti area (Welcomme and Ginsburg, 1997, and Welcomme et al., 1997), show more derived characters than the ones from Li. The first record of *P. benjavuni* in Pakistan is therefore considered to be somewhat younger than the Li locality. Comparison of the rodent associations from level 6 with those from the base of the Manchar Formation in the Gaj and Sehwan areas (Wessels, 1996) suggests that an age of 16 to 17 million years is more probable for level 6 than the 18 million years suggested by Welcomme et al. (1997).

The cheek teeth of *Kanisamys indicus* are larger and higher-crowned than those of *P. kowalskii* and *P. arifi*, so either could be ancestral to *K. indicus*.

The Miocene record of the Rhizomyidae of Pakistan shows a mosaic pattern of appearances and extinctions with the exception of *Kanisamys indicus* and *Kanisamys nagrii*, which probably are closely related and may belong to one lineage (Flynn, 1990:597). Ancestor-descendant relationships are not clear because gradual transitions between species are not documented and the ranges of species that are potentially members of one lineage (partly) overlap (Fig. 2; Flynn, 1982a, 1986). This peculiar pattern can only be explained by postulating migrations of allopatric species.

The largest diversity among the Rhizomyidae in the Manchar Formation occurs in locality H-GSP 81.14. Here *Prokanisamys arifi*, *P. major*, and *P. benjavuni*, known from older levels, are associated with the newcomer *Kanisamys indicus*. Shortly after this rhizomyid optimum the number of species drops to two: *Prokanisamys major* and *Kanisamys indicus*. These two species share a range of about five million years (see also Jacobs et al., 1989; Flynn, 1990).

The earliest adaptations to a fossorial lifestyle have been shown to occur in *Brachyrhizomys* (Flynn, 1982a; 1990) from a level of the Potwar Plateau in Pakistan that has been assigned an age of nine Ma. *Prokanisamys benjavuni*, with its incipiently hypsodont cheek teeth, M¹ without a protosinus, and lower molars with deep sinusids is known from its dentition only, but this dentition shows adaptations characterizing other fossorial rodent subfamilies (Spalacinae, Anomalomyinae). It is therefore suggested that the separation between the Rhizomyinae and the Tachyoryctinae occurred much earlier than hitherto recognized.

THE POTENTIAL OF THE RHIZOMYIDAE FOR BIOSTRATIGRAPHY

Figure 8 shows the Rhizomyidae from the Lower Manchar Formation and allows the recognition of two assemblage zones. The lower zone is characterized by the presence of *Prokanisamys arifi*. In the upper part of this zone *P. arifi* occurs associated with *P. benjavuni*, *P. major* and/or *K. indicus*. The co-occurrence of *P. major* and *K. indicus* and the absence of *P. arifi* and *P. benjavuni* characterize the upper zone.

The occurrences of several Rhizomyidae species in the succession of the Potwar Plateau (Jacobs et al., 1989) allows the recognition of three zones. In the lower zone *Prokanisamys major* and *Kanisamys indicus* co-occur, *P. arifi* and *P. benjavuni* are absent (same as the upper zone from the Lower Manchar Formation). The second zone is characterized by the replacement of *Kanisamys indicus* by its successor *K. nagrii* and the absence of *P. major*. The third zone in the Potwar Plateau is characterized by the appearance of several species of *Brachyrhizomys*.

It seems that a foursome division of the Pakistani Miocene is possible on the basis of the Rhizomyidae, but further information is needed to define formal biozones.

THE AGE OF THE GAJ AND SEHWAN ASSEMBLAGES

Since dependable palaeomagnetic data on the Gaj and the very condensed Sehwan sections are not available, age estimates of our assemblages are based on biostratigraphical correlation with assemblages from the Potwar region and the Sulaiman range which are tied to palaeomagnetic data.

Difficulties in recognizing similarities in the composition of assemblages are as follows: differences in taxonomic identification and interpretation by different authors; absence of information on the intraspecific variation (either due to stasis or to lack of description of this variation); variation differences due to geographical distribution, preservation, sedimentation (sorting) and/or sampling method.

Correlations of the Sehwan and Gaj faunas based on the preliminary faunal lists by de Bruijn et al. (1984) have been suggested by several authors (i.e., Bernor et al., 1988; Lindsay and Downs, 1998; Jacobs et al., 1989). More precise correlations will not be possible before all the material will have been correctly identified and the intraspecific variation known. Wessels (1996) gave conservative age estimates, based on the detailed comparison of the Myocricetodontinae from the Potwar region with those from Sind. The Sehwan localities were then considered to have ages between 13.7 and 16.2 Ma, the upper Gaj locality younger than 13.7, and the lower Gaj localities older than 16.2 Ma but younger than the Murree assemblage.

Lindsay (1996) concluded, on basis of the Rhizomyidae, that the locality from the base of the Murree Formation near Banda Daud Shah is slightly younger than

locality Z 113 from the Pinda Zir Dome (Sulaiman Range), which is dated at approximately 20 Ma. We follow Lindsay and consider the lower Gaj localities to have ages between 16.2 and 19.5 Ma.

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LITERATURE CITED

- BERNOR, R. L., L. J. FLYNN, T. HARRISON, S. T. HUSSAIN, AND J. KELLEY. 1988. *Dionysopithecus* from southern Pakistan and the biochronology and biogeography of early Eurasian catarrhines. *Journal of Human Evolution*, 17:339–358.
- BLACK, C. C. 1972. Review of Fossil rodents from the Neogene Siwalik beds of India and Pakistan. *Paleontology*, 15(2):238–266.
- BRUIJN, H. DE, AND S. T. HUSSAIN. 1984. The succession of rodent faunas from the Lower Manchar Formation, Southern Pakistan and its relevance for the biostratigraphy of mediterranean Miocene. *Paléobiologie continentale*, XIV(2):191–202.
- . 1985. *Thryonomyidae* from the Lower Manchar Formation of Sind, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 88(2):155–166.
- BRUIJN, H. DE, AND G. SARAÇ. 1991. Early Miocene rodent faunas from the western Mediterranean area. Part I. The genus *Eumyarion*. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 94(1):1–36.
- BRUIJN, H. DE, E. BOON, AND S. T. HUSSAIN. 1989. Evolutionary trends in *Sayimys* (Ctenodactylidae, Rodentia) from the Lower Manchar Formation (Sind, Pakistan). *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 92(3):191–214.
- BRUIJN, H. DE, S. T. HUSSAIN, AND J. J. M. LEINDERS. 1981. Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 84(1):71–99.
- CARLETON, M. D., AND G. G. MUSSER. 1984. Muroid rodents. Pp. 289–379, in *Orders and families of recent mammals of the World* (S. Anderson and J. K. Jones, eds.). John Wiley, New York.
- CHALINE, J. P. MEIN, AND F. PETTER. 1977. Les grandes lignes d'une classification évolutive des Muroidea. *Mammalia*, 41:245–252.
- DEHM, R., L. L. JACOBS, W. WESSELS, H. DE BRUIJN, AND S. T. HUSSAIN. 1982. Fossil rodents from the type area of the Chinji Formation, Siwalik group, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 85(3):259–263.
- DOWNING, K. F., E. H. LINDSAY, W. R. DOWNS, AND S. E. SPEIJER. 1993. Lithostratigraphy and vertebrate biostratigraphy of the early Miocene Himalayan Foreland, Zinda Pir Dome, Pakistan. *Sedimentary Geology*, 87:25–37.
- FAHLBUSCH, V. 1964. Die cricetiden (Mammalia) der Oberen Süßwasser-Molasse bayerns. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge*, 118:1–136.
- FLYNN, L. J. 1982a. Systematic revision of Siwalik Rhizomyidae (Rodentia). *Geobios*, 15(3):327–389.
- . 1982b. A revision of fossil rhizomyid rodents from northern India and their relation to a rhizomyid biochronology of Pakistan. *Geobios*, 15:583–588.
- . 1986. Species longevity, stasis and stairsteps in rhizomyid rodents. Pp. 273–285, in *Vertebrates, phylogeny and philosophy* (M. Flanagan and J. A. Lillegraven, eds.). *Contributions in Geology*, University of Wyoming, Special Paper, 3.

- . 1990. The natural history of Rhizomyid rodents. Pp. 155–183, in *Evolution of subterranean mammals at the organismal and molecular levels* (E. Nevo, and O. A. Reig, eds.). A. R. Liss, Inc., New York.
- JACOBS, L. L., L. J. FLYNN, AND W. R. DOWNS. 1989. Neogene rodents of Southern Asia. Pp. 157–177, in *Papers on fossil rodents in honor of Albert E. Wood* (C. C. Black and M. R. Dawson, eds.). Los Angeles County Museum Sciences series, 33.
- KALTHOFF, D. C. 1999. Die Schmelzmikrostruktur in den Incisiven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). Ph.D. Thesis, Bonn, Germany.
- KLEINHOFMEIJER, G., AND H. DE BRUIJN. 1988. The mammals from Aliveri (island of Evia, Greece). Part 8. The Cricetidae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 91(2):185–204.
- LARTET, E. 1851. Notice sur la colline de Sansan. 1 volume. J. -A. Portes, Auch.
- LINDSAY, E. H. 1996. A new eumyarionine cricetid from Pakistan. *Acta zoologica Cracoviensis*, 39(1): 279–288.
- LINDSAY, E. H., AND W. R. DOWNS. 1998. Cricetid rodents from Miocene Deposits of Pakistan. I. Pp. 35–47, in *3e Geosas workshop, Pakistan* (Ghaznov, S. M. Raza and M. T. Hasan, eds.).
- MEIN, P., AND M. FREUDENTHAL. 1971. Les cricetidae de Vieux-Collonges. *Partie I. Scripta Geologica*, 5.
- MEIN, P., AND L. GINSBURG. 1985. Les rongeurs miocènes de Li (Thaïlande). *Comptes Rendus de l'Académie des Sciences, Paris*, t. 301, II, 19:1369–1374.
- . 1997. Les mammifères du gisement Miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. *Geodiversitas*, 19(4):783–844.
- MILLER, G. S., AND J. W. GIDLEY. 1918. Synopsis of supergeneric groups of rodents. *Journal of the Washington Academy of Sciences*, 8:431–448.
- MUNTHE, J. 1980. Rodents of the Miocene Daud Khel Local fauna, Mianwali District, Pakistan. Part II. Sciuridae, Gliiridae, Ctenodactylidae and Rhizomyidae. *Milwaukee Public Museum, Contributions in Biology and Geology*, 34:1–36.
- NEVO, A. 1999. Mosaic evolution of subterranean mammals. Regression, progression and global convergence. Oxford University Press, Oxford, United Kingdom.
- NOWAK, R. M. 1991. Walker's mammals of the World. Fifth edition. J. Hopkins University Press, London, United Kingdom.
- PRASAD, K. N. 1968. The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, 39:1–56.
- SCHAUB, S. AND H. ZAPFE. 1953. Die Fauna der miozänen Spaltenfüllung von Neudorf a. d. March. *Simplicidentata. Sitzungsbereich der Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse*, 162(1):181–215.
- ÜNAY-BAYRAKTAR, E. 1989. Rodents from the middle Oligocene of Turkish Thrace. *Utrecht Micropaleontological Bulletins, Special Publication*, 5.
- WELCOMME, J-P., P-O. ANTOINE, F. DURANTHON, P. MEIN, AND L. GINSBURG. 1997. Nouvelles découvertes de Vertébrés miocènes dans le synclinal de Dera Bugti (Balouchistan, Pakistan). *Comptes rendus de l'Académie des Sciences, Paris*, 325:531–536.
- WELCOMME, J-P., AND L. GINSBURG. 1997. Mise en évidence de l' Oligocene sur le territoire des Bugti (Balouchistan, Pakistan). *Comptes rendus de l'Académie des Sciences, Paris*, 325:999–1004.
- WU, W. 1982. Die Cricetiden (Mammalia, Rodentia) aus der Oberen Süßwasser-Molasse von Puttenhausen (Niederbayern). *Zitteliana*, 9:37–80.
- WESSELS, W. 1996. Myocricetodontinae from the Miocene of Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 99(3–4):253–312.
- WESSELS, W., H. DE BRUIJN, S. T. HUSSAIN, AND J. J. M. LEINDERS. 1982. Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 85(3):337–364.
- WESSELS, W., E. ÜNAY, AND H. TOBIEN. 1987. Correlation of some Miocene faunas from Northern Africa, Turkey and Pakistan by means of Myocricetodontinae. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, B, 90(1):65–82.
- WOOD, A. E. 1937. Fossil rodents from the Siwalik beds of India. *American Journal of Sciences*, New Haven, 36:64–76.

APPENDIX 1

Material and measurements of Prokanisamys arifi.

Locality		Length			Width		
		N	Mean	Range	N/N	Mean	Range
H-GSP 8426	M ¹	1	20.4		1/1	15.6	
H-GSP 8114	M ¹	0			0/0		
H-GSP 8424	M ¹	0			0/0		
H-GSP 8114a	M ¹	1			0/0		
H-GSP 8106	M ¹	4	19.200		1/2	14.500	14.3–14.7
H-GSP 8311	M ¹	9	19.750	18.0–20.9	5/6	14.967	14.6–15.6
H-GSP 8107 (a)	M ¹	1			0/0		
H-GSP 8426	M ²	0			0/0		
H-GSP 8114	M ²	0			0/0		
H-GSP 8424	M ²	0			0/0		
H-GSP 8114a	M ²	9	14.857	14.0–15.9	7/9	14.611	13.1–16.5
H-GSP 8106	M ²	5	14.650	14.1–15.2	4/3	14.300	13.6–14.9
H-GSP 8311	M ²	14	14.920	14.3–15.6	10/10	14.240	13.4–15.3
H-GSP 8107 (a)	M ²	5	15.125	14.4–15.8	3/3	14.500	13.1–15.3
H-GSP 8426	M ³	2	12.350	11.2–13.5	2/2	13.050	12.4–13.7
H-GSP 8114	M ³	4	12.600	12.0–13.2	2/2	12.950	12.9–13.0
H-GSP 8424	M ³	6	11.933	11.5–12.5	3/3	12.200	11.8–12.6
H-GSP 8114a	M ³	3	12.700	11.9–13.7	3/3	13.600	12.9–14.7
H-GSP 8106	M ³	5	12.450	11.8–13.4	4/4	12.675	11.9–13.7
H-GSP 8311	M ³	16	11.486	10.3–12.4	14/14	12.200	11.5–13.3
H-GSP 8107 (a)	M ³	3	11.900	11.5–12.5	3/2	12.600	12.4–12.8
H-GSP 8426	M ₁	3	17.550	17.0–18.1	2/2	12.900	12.4–13.4
H-GSP 8114	M ₁	2	18.200		1/1	10.800	
H-GSP 8424	M ₁	1	17.000		1/1	11.200	
H-GSP 8114a	M ₁	5	18.133	17.7–18.6	3/4	12.650	11.2–13.4
H-GSP 8106	M ₁	6	18.333	17.8–19.0	3/3	12.700	12.5–12.8
H-GSP 8311	M ₁	15	17.510	16.8–18.2	10/9	11.944	10.9–12.9
H-GSP 8107 (a)	M ₁	7	18.450	18.1–18.7	4/5	12.660	12.0–13.2
H-GSP 8426	M ₂	1	15.000		1/0		
H-GSP 8114	M ₂	0			0/0		
H-GSP 8424	M ₂	1			0/0		
H-GSP 8114a	M ₂	6	16.700		1/2	15.050	14.8–15.3
H-GSP 8106	M ₂	8	15.750	15.1–16.1	6/5	14.020	13.2–14.6
H-GSP 8311	M ₂	18	15.762	14.4–17.4	13/14	14.136	13.1–15.9
H-GSP 8107 (a)	M ₂	11	16.4	15.6–17.5	6/7	14.471	13.5–15.5
H-GSP 8426	M ₃	3			0/0		
H-GSP 8114	M ₃	0			0/0		
H-GSP 8424	M ₃	5	14.275	13.5	4/3	13.167	12.9–13.7
H-GSP 8114a	M ₃	2			0/1	12.500	
H-GSP 8106	M ₃	9	14.280	13.8–14.7	5/4	12.700	11.8–13.3
H-GSP 8311	M ₃	15	14.985	13.8–16.4	13/15	12.460	11.4–13.5
H-GSP 8107 (a)	M ₃	4	14.9	14.4–15.4	2/3	13.000	12.0–14.1

In 0.1-mm units.

APPENDIX 2

Length/Width ratios of several Eumyarion and Prokanisamys species.

Species	L/W M ¹	L/W M ²	L/W M ₁	L/W M ₁	Localities source of data
<i>Eumyarion medium</i> (Lartet, 1851)	40 1.39	42 1.00	28 1.59	33 1.20	Sansan Coll. UU
<i>Eumyarion latior</i> (Schaub and Zapfe, 1953)	8/9 1.40	8 1.08	9 1.60	7 1.27	Aliveri Kleinhofmeijer and de Bruijn, 1988
<i>Eumyarion bifidus</i> (Fahlbusch, 1964)	10 1.52	10 1.10	10 1.68	10 1.21	Sandelzhausen Coll. München
<i>Eumyarion bifidus</i>	62/57 1.55	67 1.11	65 1.66	53/54 1.25	Puttenhausen Wu, 1982
<i>Eumyarion montanus</i> de Bruijn and Saraç, 1991	65/66 1.49	59/58 1.09	57/58 1.62	65 1.24	Keseköy De Bruijn and Saraç, 1991
<i>Eumyarion carbonicus</i>	63/64 1.61	69/68 1.08	63/64 1.59	75/76 1.20	Harami 1 De Bruijn and Saraç, 1991
<i>Eumyarion aff. carbonicus</i>	6/8 1.50	7/6 1.06	11/12 1.58	9 1.32	Harami 3 De Bruijn and Saraç, 1991
<i>Prokanisamys arifi</i> de Bruijn et al., 1981	6 1.39	6/4 1.0	6 1.49	11 1.15	H-GSP 116 De Bruijn et al., 1982
<i>Prokanisamys arifi</i>	5/6 1.32	10 1.05	10/9 1.47	13/14 1.11	H-GSP 8311 This article
<i>Prokanisamys major</i> n. sp.	2 1.31	1 1.07	2 1.41	5/4 1.12	H-GSP 8224 This article
<i>Prokanisamys major</i>	2 1.30	1 1.03	1 1.44	—	H-GSP 8114 This article
<i>Prokanisamys benjavuni</i> (Mein and Ginsburg, 1985)	19 1.21	14/13 1.05	13/14 1.49	16/15 1.20	Li Mein and Ginsburg, 1997
<i>Prokanisamys benjavuni</i>	5 1.21	3 0.95	3/5 1.48	5/4 1.00	H-GSP 8114 This article
<i>Prokanisamys benjavuni</i>	3/2 1.26	2/3 1.08	2 1.40	3 1.09	H-GSP 8424 This article
<i>Prokanisamys kowalskii</i> (Lindsay, 1996)	9/12 1.40	10/12 1.01	5/6 1.40	5/4 1.11	z 113 Lindsay, 1996

APPENDIX 3

*Material and measurements of Prokanisamys major nov. sp.**Prokanisamys major*

Locality		Length			Width		
		N	Mean	Range	N/N	Mean	Range
H-GSP 8214	M ¹	1			0/0		
H-GSP 8224	M ¹	2	22.200		1/1	17.000	
H-GSP 8427	M ¹	0					
H-GSP 8227	M ¹	0					
H-GSP 8425	M ¹	0					
H-GSP 8114	M ¹	2	21.000	21.0–21.0	2/2	16.050	15.9–16.2
H-GSP 8106	M ¹	1			0/1	15.7	
H-GSP 8214	M ²	0					
H-GSP 8224	M ²	1	18.000		1/1	16.900	
H-GSP 8427	M ²	0					
H-GSP 8227	M ²	2	16.900		1/1	16.900	
H-GSP 8425	M ²	0					
H-GSP 8114	M ²	1	16.100		1/1	15.600	
H-GSP 8106	M ²	2	16.150	16.0–16.3	2/2	15.150	14.3–16.0
H-GSP 8214	M ³	2	15.700		1/1	15.400	
H-GSP 8224	M ³	7	15.275	14.5–16.0	4/4	16.300	16.0–16.6
H-GSP 8427	M ³	1	16.600		1/1	17.300	
H-GSP 8227	M ³	4	15.500	15.2–15.8	2/2	16.000	15.6–16.4
H-GSP 8425	M ³	0					
H-GSP 8114	M ³	5	15.350	14.6–16.1	2/2	17.100	16.0–18.2
H-GSP 8106	M ³	0					
H-GSP 8214	M ₁	1	19.500		1/1	14.600	
H-GSP 8224	M ₁	4	21.500	21.2–21.8	2/2	15.033	14.1–16.1
H-GSP 8427	M ₁	0					
H-GSP 8227	M ₁	3	19.267	19.0–19.4	3/3	14.200	13.7–14.9
H-GSP 8425	M ₁	1	20.600		1/1	14.500	
H-GSP 8114	M ₁	4	19.400		1/1	13.500	
H-GSP 8106	M ₁	0					
H-GSP 8214	M ₂	1	18.500		1/1	16.800	
H-GSP 8224	M ₂	9	19.640	17.5–21.3	5/4	17.525	15.6–18.8
H-GSP 8427	M ₂	1	18.500		1/1	16.800	
H-GSP 8227	M ₂	1	20.200		1/1	17.000	
H-GSP 8425	M ₂	0					
H-GSP 8114	M ₂	1			0/0		
H-GSP 8106	M ₂	1	17.7		1/1	16.2	
H-GSP 8214	M ₃	0					
H-GSP 8224	M ₃	1	16.300		1/1	16.300	
H-GSP 8427	M ₃	1			0/0		
H-GSP 8227	M ₃	1			0/0		
H-GSP 8425	M ₃	0					
H-GSP 8114	M ₃	9	15.057	13.4–16.4	7/6	13.300	12.7–14.1
H-GSP 8106	M ₃	2	16.800		1/1	13.800	

In 0.1-mm units.

APPENDIX 4

Material and measurements of Prokanisamys benjavuni.

Locality		Length			Width		
		N	Mean	Range	N/N	Mean	Range
H-GSP 8426	M ¹	1			0/1	14.800	
H-GSP 8114	M ¹	5	19.580	18.1–21.2	5/5	16.140	15.2–17.6
H-GSP 8424	M ¹	7	18.600	17.8–19.7	3/2	14.800	14.6–15.0
H-GSP 8114a	M ¹	4	19.650	19.0–20.4	4/4	16.250	14.3–18.1
H-GSP 8426	M ²	2	17.950	17.9–18.0	2/2	16.900	13.6–17.2
H-GSP 8114	M ²	3	15.133	14.6–15.4	3/3	15.933	15.0–16.5
H-GSP 8424	M ²	3	16.900	16.6–17.2	2/3	15.633	15.0–16.2
H-GSP 8114a	M ²	5	16.375	15.3–17.7	4/4	17.525	16.3–18.4
H-GSP 8426	M ³	2	17.000		1/1	16.700	
H-GSP 8114	M ³	8	16.383	15.7–17.1	6/6	16.083	15.0–17.7
H-GSP 8424	M ³	2	17.800		1/1	17.7	
H-GSP 8114a	M ³	1	16.600		1/1	16.000	
H-GSP 8426	M ₁	1	19.400		1/1	12.500	
H-GSP 8114	M ₁	6	19.467	19.3–19.6	3/5	13.200	12.1–14.0
H-GSP 8424	M ₁	5	18.600	18.5–18.7	2/2	13.250	12.5–14.0
H-GSP 8114a	M ₁	1			0/1	12.900	
H-GSP 8426	M ₂	3	16.333	16.0–16.6	3/3	15.167	14.1–16.1
H-GSP 8114	M ₂	6	16.700	16.2–17.6	5/4	16.625	15.6–17.5
H-GSP 8424	M ₂	6	17.300	17.1–17.5	3/3	15.933	14.4–17.1
H-GSP 8114a	M ₂	6	18.060	16.5–19.7	5/5	17.300	16.2–18.4
H-GSP 8426	M ₃	7	19.067	17.6–20.1	3/5	15.900	14.7–17.1
H-GSP 8114	M ₃	5	18.350	17.6–18.7	4/4	15.275	14.1–16.3
H-GSP 8424	M ₃	7	19.133	16.5–21.2	3/4	15.300	14.1–16.9
H-GSP 8114a	M ₃	7	19.150	17.6–21.3	4/4	15.975	15.3–16.5

In 0.1-mm units.

APPENDIX 5

Material and measurements of ?Prokanisamys sp. A.

Locality		Length			Width		
		N	Mean	Range	N/N	Mean	Range
H-GSP 8107 (a)	M ¹	1			0/0		
	M ²	0					
	M ³	0					
	M ₁	1	20.800		1/1	14.100	
	M ₂	1	18.200		1/0		
	M ₃	2	19.800		1/2	16.800	16.3–17.3

In 0.1-mm units.

APPENDIX 6

Material and measurements of Kanisamys indicus.

<i>Kanisamys indicus</i>		Length			Width		
Locality		N	Mean	Range	N/N	Mean	Range
H-GSP 8214	M ¹	0					
H-GSP 8224	M ¹	3	23.867	22.9–24.9	3/3	19.233	18.3–20.1
H-GSP 8427	M ¹	3	23.000		1/3	18.250	18.2–18.3
H-GSP 8227	M ¹	2	24.800		1/2	18.850	17.9–19.8
H-GSP 8425	M ¹	0					
H-GSP 8114	M ¹	5	23.767	22.0–24.8	3/4	17.950	17.0–18.7
H-GSP 8214	M ²	2	19.200	19.1–19.3	2/2	19.750	19.1–20.4
H-GSP 8224	M ²	8	18.440	17.9–19.8	5/6	19.250	18.3–19.8
H-GSP 8427	M ²	0					
H-GSP 8227	M ²	2	21.200		1/2	19.750	19.0–20.5
H-GSP 8425	M ²	2	19.400		1/1	20.800	
H-GSP 8114	M ²	1	20.000		1/1	19.600	
H-GSP 8214	M ³	1	16.700		1/1	18.600	
H-GSP 8224	M ³	5	17.925	17.2–19.2	4/4	19.500	17.8–21.8
H-GSP 8427	M ³	0					
H-GSP 8227	M ³	1	18.500		1/1	19.200	
H-GSP 8425	M ³	1			0/0		
H-GSP 8114	M ³	1			0/0		
H-GSP 8214	M ₁	0					
H-GSP 8224	M ₁	5	22.775	22.3–23.3	4/3	17.733	16.8–18.4
H-GSP 8427	M ₁	0					
H-GSP 8227	M ₁	1	22.100		1/1	16.700	
H-GSP 8425	M ₁	0					
H-GSP 8114	M ₁	0					
H-GSP 8214	M ₂	0					
H-GSP 8224	M ₂	4	22.400	21.2–23.6	2/2	21.500	21.0–22.0
H-GSP 8427	M ₂	0					
H-GSP 8227	M ₂	4	21.000	19.6–21.7	3/4	19.750	19.0–20.2
H-GSP 8425	M ₂	1			0/1	19.800	
H-GSP 8114	M ₂	0					
H-GSP 8214	M ₃	0					
H-GSP 8224	M ₃	9	22.183	20.8–24.2	6/6	19.483	18.2–21.8
H-GSP 8427	M ₃	0					
H-GSP 8227	M ₃	9	21.400	20.4–22.2	3/5	18.280	16.9–18.8
H-GSP 8425	M ₃	2			0/0		
H-GSP 8114	M ₃	4	21.333	19.3–22.6	3/1	18.000	

In 0.1-mm units.

APPENDIX 7

 M_1/M_3 ratio.

Width M_1/M_3	<i>P. arifi</i>	<i>P. major</i>	<i>P. benjavuni</i>	<i>K. indicus</i>
H-GSP 8214				
H-GSP 8224		0.92		0.91
H-GSP 8427				
H-GSP 8227				0.91
H-GSP 8426			0.79	
H-GSP 8425				
H-GSP 8114		1.12	0.86	
H-GSP 8424	0.84		0.87	
H-GSP 8114a	1.01		0.81	
H-GSP 8106	1.00			
H-GSP 8311	0.96			
H-GSP 8107 (a)	0.97			

MURREE *Prokanisamys arifi* 1.03.THAILAND *Prokanisamys benjavuni* 0.84.ZINDA PIR DOME *Prokanisamys kowalskii* 0.94.POTWAR PLATEAU *Prokanisamys major* (specimen 26046, loc 640) 0.93.

APPENDIX 8

Area occlusal surface M_1 /Area occlusal surface $M_3 \times 100$.

Area M_1 /Area M_3 $\times 100$	<i>P. arifi</i>	<i>P. major</i>	<i>P. benjavuni</i>	? <i>P. sp.A</i>	<i>K. indicus</i>
H-GSP 8214					
H-GSP 8224		121			93
H-GSP 8427					
H-GSP 8227					94
H-GSP 8426			80		
H-GSP 8425					
H-GSP 8114		130	91		
H-GSP 8424	101		85		
H-GSP 8114a					
H-GSP 8106	128				
H-GSP 8311	111				
H-GSP 8107 (a)	121			88	

MURREE *Prokanisamys arifi* 127.THAILAND *Prokanisamys benjavuni* 86.ZINDA PIR DOME *Prokanisamys kowalskii* 111.POTWAR PLATEAU (specimen 26046, loc 640) *Prokanisamys major* 104.

APPENDIX 9

Area occlusal surface M².

Area M ² In 0.1-mm units	<i>P. arifi</i>	<i>P. major</i>	<i>P. benjavuni</i>	<i>K. indicus</i>
H-GSP 8214				379.20
H-GSP 8224		304.2		354.97
H-GSP 8427				
H-GSP 8227		285.61		418.70
H-GSP 8426			304.20	
H-GSP 8425				403.52
H-GSP 8114		251.16	241.60	392.00
H-GSP 8424			263.64	
H-GSP 8114a	217.54		287.00	
H-GSP 8106	231.81	246.24		
H-GSP 8311	211.58			
H-GSP 8107 (a)	218.95			

MURREE *Prokanisamys arifi* 204.49.THAILAND *Prokanisamys benjavuni* 298.8.ZINDA PIR DOME *Prokanisamys kowalskii* 282.23.POTWAR PLATEAU *Prokanisamys major* (specimen 26042) 264.

APPENDIX 10

Area occlusal surface M₂.

Area M ₂ In 0.1-mm units	<i>P. arifi</i>	<i>P. major</i>	<i>P. benjavuni</i>	<i>K. indicus</i>
H-GSP 8214		310.80		
H-GSP 8224		343.00		481.60
H-GSP 8427		310.80		
H-GSP 8227		343.40		414.75
H-GSP 8426			247.76	
H-GSP 8425				
H-GSP 8114			277.22	
H-GSP 8424			275.07	
H-GSP 8114a	252.17		313.30	
H-GSP 8106	221.20	286.74		
H-GSP 8311	222.78			
H-GSP 8107 (a)	237.80			

MURREE *Prokanisamys arifi* 213.52.THAILAND *Prokanisamys benjavuni* 266.71.ZINDA PIR DOME *Prokanisamys kowalskii* 286.58.POTWAR PLATEAU *Prokanisamys major* (specimen 26046) 351.

APPENDIX 11

Prokanisamys arifi

Maximum of measured crown height of protocone(id)/hypocone(id)

	Murree	H-GSP 8107	H-GSP 8311	H-GSP 8106	H-GSP 8114a	H-GSP 8114	H-GSP 8424	H-GSP 8426
M ¹	10.3/11.5	9.5/9.5	11.1/12.4	10.0/11.1	7.4/8.0			8.8/8.8
M ²	9.5/9.0	10.0/10.8	10.7/10.0	11.5/10.3	16.0/13.6			
M ³	9.0	9.0	9.9	8.7	8.4	10.8	12.5	11.6
M ₁	7.4/9.8	8.8/9.2	8.0/8.6	7.4/9.8	10.2/8.7	7.9/7.9		5.9/5.9
M ₂	8.7/8.9	9.5/9.5	10.7/10.5	9.2/8.2	9.5/10.1		7.0	
M ₃	8.5/8.0	9.5/9.0	8.2/7.8	9.2/8.2			12.5	12.4

In 0.1-mm units

Prokanisamys major

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8106	H-GSP 8114	H-GSP 8425	H-GSP 8227	H-GSP 8224	H-GSP 8214
M ¹		10.5/8.8			14.9/14.5	
M ²	10.7/10.3	9.6/—			13.6/12.4	
M ³		9.2		7.9	11.0	14.0
M ₁	7.8/9.3		8.3/—		9.2/—	9.0/10.5
M ₂	10.4/9.2	10.5/—		8.3/—	8.2/—	9.1/10.5
M ₃		9.1		9.0	10.0	

In 0.1-mm units

Prokanisamys benjavuni

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8114a	H-GSP 8424	H-GSP 8114	H-GSP 8426
M ¹	14.0/16.6	14.3/14.3	12.4/13.1	—/16.6
M ²	6.6/15.3	17.4/16.8	14.0/13.3	15.4/14.7
M ³	15.7	9.5	13.4	13.0
M ₁	9.1/11.8	12.2/8.0	11.5/11.5	7.8/10.5
M ₂	13.5/15.2	10.6/—	11.6/13.5	14.0/11.0
M ₃		11.6	13.2/13.0	10.7/9.6

In 0.1-mm units

Kanisamys indicus

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8114	H-GSP 8425	H-GSP 8227	H-GSP 8427	H-GSP 8224	H-GSP 8214
M ¹	13.2/15.6		13.3/14.3	14.1/13.3	14.5/15.4	
M ²	11.4/9.6		15.0/15.0		14.4/15.5	14.0/14.0
M ³			12.5		20.6	4.1
M ₁			10.5/12.6		14.5/15.4	
M ₂		8.3/—	12.3/12.3		9.6	
M ₃	13.8/15.0	7.0	13.6/13.4		16.0/17.8	

In 0.1-mm units

? Prokanisamys sp. A

Maximum of measured crown height of protocone(id)/hypocone(id)

	H-GSP 8107 (a)
M ¹	9.5/9.5
M ²	
M ³	
M ₁	16.8/19.8
M ₂	
M ₃	8.3/9.2

In 0.1-mm units